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Thesis

THE GRAFT UNION: AN ANALYSIS OF THE RECIPROCAL EFFECT OF STOCK AND SCION

Submitted by

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INTRODUCTION

Our heritage from earliest historical agriculture included the science of grafting. That the gardeners of the Caesars were familiar with the technique of grafting is indisputable, and that the practice extended far back into shadowy antiquity is very probable. We find some rather unscientific references to grafting in Virgil and Pliny, while Cato (Cap. 42) and Columella (Lib. IX) take the matter up in some detail.

Because of its vital importance to agriculturists, it is not strange that the literature of the last few centuries should contain many references to grafting and budding, and often references showing surprisingly careful observation and penetration. But the growing importance of the wholesale grafting of fruit trees and ornamentals today has quite eclipsed the work of the past. There is no fruit tree in America which is not customarily grown on other roots than its own, and with many ornamental trees and shrubs the same is likewise true.

The records also show an early recognition of compatibility and incompatibility in the graft. As commonly understood, <u>compatibility is perfect when a graft acts as though the stock</u>

were grafted with a scion of itself, union being perfect, and the behavior of the plant the same as that of an entire, ungrafted plant under the influence of the same environment. Any development short of this would be termed incompatibility or uncongeniality. The phenomena are essentially the same whether the scion be a twig bearing several buds (grafting) or a single bud (budding or inoculation). Likewise they are the same whether the scion is inserted into a sapling-stock or tree-stock, near the ground (grafting proper), or whether many or all of the ultimate branches are grafted with scions from another plant (top-working).

While compatibility and various degrees of incompatibility have been observed by everyone who has practiced grafting, there has been uncertainty as to the underlying principles. A fundamental, satisfying explanation of these phenomena is in general lacking. It is this problem of accounting for incompatibility in certain specific instances that has presented itself to me in the course of researches on diseases of lilacs. As a part of my work, I have assembled and attempted to analyze contributions of various investigators that have a bearing on the problem of reciprocal effect between stock and scion.

GENETIC RELATIONSHIP, A FACTOR IN GRAFTING

One of the primary factors entering into the problem of compatibility in grafting is that of the natural relationship between stock and scion. The question in this connection is the extent of the correlation that exists between natural or genetic relationship and compatibility. The earlier literature

is replete with impossible claims of successful grafting of plants genetically far removed from one another, as that of the pear on the oak, the pear on the maple, the mulberry on the elm. But in 1788 we find DUHAMEL DU MONCEAU (22) asserting that all species of trees cannot be grafted onto each other, and that "cette union ne se peut faire que lorsqu'il y a une certaine analogie entre la greffe et la sujet." Experience has taught that there is a range of relationships outside of which successful grafting is not possible, and that within this range there are varying degrees of compatibility.

The difficulty of generalizing, i.e. of expressing a covering formula, lies in the fact that taxonomy is based on superficial resemblances and not on physiological reactions; and since the artificial symbiosis effected by the graft is apparently a physiological phenomenon, a certain amount of divergence in given instances might not affect the general proposition. Phylogenetic relationship is undoubtedly a matter of physiological as well as of morphological resemblances; but, owing to the great difficulty in using physiological reactions as a basis of taxonomy, and the comparative ease of morphological determinations, there has been a great tendency to stress the external morphological side of phylogeny at the expense of the physiological. Convergent evolution may produce very similar structures in species which are only distantly related in the phylogenetic tree. NUTTALL's exhaustive experiments in immunological reactions (58: 1908) have likewise suggested that a safe key to relationship may be physiological. DANIEL (16: 1899) appreciated this when he wrote: "One can see that the principle of relationship can be established only if the

botanical classification is based on the similarities of protoplasm and on its functional capacities, which is far from being the case."

A number of attempts have been made to formulate definitely the limits of the possibility of grafting. In 1841 KNIGHT (44) suggested that all grafts should be interspecific and that only close relatives in the species should be grafted. SAHUT (75,77: 1885), observing the limitations imposed by the requirements of relationship, asserted that the absolute possibility of grafting exists only between varieties of a single species, but that it often extends between species belonging to different genera of the same family, and exceptionally between species of different families. As an example of this last possibility, DANIEL (14: 1891) mentions grafts of _Saponaceae_ on _Onagraceae_, although as an exception to the rule that the closer the relationship, the greater the probability of success. Similarly, BAILEY (4: 1898) notes that although close botanical relationship is usually an essential to the success of the graft, this relationship is by no means a safe guide. Among Cacti, for example, the leafless _Epiphyllum_ grows remarkably well on the leaf-bearing _Pereskia_, although the two are plants of very distinct genera. LINDEMUTH (50: 1901) likewise records some exceptions to the principle of genetic relationship. Thus _Solanum tuberosum_ on _S. pseudocapsicum_ is incompatible, while _S. tuberosum_ on _Datura_ and _Physalis_ is quite the opposite. Apple (_Prunus malus_) on pear (_P. communis_) never succeeds, but _P. communis_ on _Cydonia_, _Crataegus_, _Sorbus_, and _Mespilus_ are generally successful. On the other hand, inter-

varietal grafts need not necessarily be successful, according to HEPPNER and McCALLUM (36: 1927), as witness the failure of most European plums on most Japanese plums. Genetic relationship, although a fair guide to congeniality, is by no means infallible. BURBANK (12: 1909) has drawn a suggestive comparison between the possibilities of grafting and of hybridization of two plants; and although the analogy is not perfect, it is significant.

Although BREGGER (10: 1924) feels the evidence insufficient to establish the claim that grafting success is dependent on the genetic constitution of the roots, it is the consensus of opinion of many workers, e.g. HOWE (40: 1929), WEBBER (92: 1926), and BROWN (11: 1916), that the closeness of genetic relationship exercises a fundamental influence on congeniality, of such a nature that there is a definite and positive correlation between genetic analogy of stock and scion and compatibility.

REASONS ADVANCED FOR THE FAILURE OF GRAFTS

There have been many attempted explanations for the lack of success of certain grafts, and these will be considered in the pages immediately following. It should be borne in mind, however, that the suggestions are far from equal in value and in supporting evidence. In fact the problem has not undergone the careful analysis it deserves, for the most part, but has often been summarily passed off with a few superficial statements; while only rarely has it been the stimulus to painstaking scientific investigation.

1. Faulty technique

For the graft to succeed it is obvious that the technical procedure must be in harmony with the needs of stock and scion, and with the theory of grafting. Since union takes place through the activity of the cambium layer of cells, it would seem essential that the cambia of stock and scion should be in close contact. This detail has certainly been known since the earliest days of grafting. The union may be accomplished in a variety of ways, all of which, however, require that a large area of cambium cells be placed in juxtaposition to a corresponding area of cambium cells in the other biont. It is presupposed that the grafts in question are made in the approved manner, and with due regard to avoidance of drying and infection. Failure to observe these details would certainly cause lack of success in the graft, but such failures would not pertain directly to the problem of compatibility.

Numerous minor details of the grafting operation have been offered as possible causes of difficult union. For example, in 1925 ROBERTS (72) suggested that since the growth of the scion is usually from the top bud, since the callus union is best along the tongues of the graft, and since the rapid rise of water during transpiration is in a straight line with slow lateral diffusion, the top bud of the scion should be directly above the point of union. The following year (1926) BENNETT (6) found, on the contrary, that there was little evidence to indicate that the position of the terminal bud relative to the graft union had any bearing on the resultant stand of the grafted trees or the amount of growth produced under the conditions of his experiment.

Whatever detrimental influences may arise from this item of technique, it is doubtless trivial compared to the more fundamental causes of uncongeniality.

More recently MELHUS, MUNCIE, and FISK (55: 1928) observed that in a graft with an overhanging scion-lip, excess callus forms, first as a knot from the grafted cambium of the scion, later growing backward, filling the space between stock and scion. The phellogen layer, being soon differentiated in the callus, cuts off and causes the death of the outer layer of proliferating cells of the scion callus. The slower-growing stock-callus finding no meristematic cells with which to unite, lack of continuity of the union results. These observations led to trials of wedge-grafting in place of tongue-grafting as a means of holding the scion-lip in place, and thus preventing knot-formation. In experiments with several hundred trees, it was found that a very much higher percentage of the tongue-grafted trees showed callus-knots developing from the tip of the scion-lip.

RIKER, BANFIELD, and KEIST (71: 1928), observing similar knot-formation on apple trees, succeeded in controlling them by careful wrapping and fitting. This care has also the advantage of preventing girdling as a result of too tight wrapping. Investigations of a number of methods revealed the superiority of medical adhesive tape in increasing the percentage of salable trees.

In certain very difficult cases of grafting, special technique seems to offer the solution of success. KNIGHT (44: 1841), for example, gives a method of grafting the walnut, which had

previously resisted all attempts at grafting. The method consists essentially in reducing temporarily the vigor of the scion. DANIEL (20) in 1927 succeeded in grafting Myosotis palustris (True Forget-me-not) and Mertensia maritima (Sea Lungwort) on cabbage, as well as Kleinia articulata on Cineraria, by cutting the stalk so that the scion could be grafted immediately above a node with leaves. The success in these cases is partly attributed to the nutrients thus supplied.

It will be seen from the foregoing that it is not apparent that the details of grafting technique are of any great significance in the success or failure of the union. In general, WAUGH (88: 1904) compactly summarizes the question of graft weakness with reference to technique when he states that the weakness of unions results nearly always from the physiological incompatibility of the stock and scion, and very seldom from faulty manipulation in the setting of the graft.

2. Wood defects

We find the claim that mechanical weakness may be a cause underlying graft failure supported by somewhat stronger evidence. It is apparent that if the union is a point of physical weakness, the durability of the tree is likely to be unfavorably affected. It is commonly observed by nurserymen that if the stock and scion are each prepared by making a single oblique cut, the graft resulting from the union of these two plane surfaces is notably weaker than if the bionts are so cut that they dovetail together. Breakage at the line of union is a fairly common phenomenon in the early stages of the symbiosis. But given reasonable care at first, the question arises whether this

mechanical weakness is a permanent characteristic of the graft.

BOOTH (9) in 1913 cut strips of wood from the interior of grafted tissue and applied pressure to them in order to determine the breaking point. He found that this does not as a rule occur at the line of union; but, considering the tree as a whole, his results are not conclusive, for WEBBER (92) in 1926 has shown that in incompatible grafts the diameter of the scion frequently exceeds that of the stock by a considerable amount. Since BOOTH was dealing with isodiametric strips of wood, his results would hardly obtain in the orchard.

WAUGH (88: 1904) found on careful investigation that in hardwood graftage, stock and scion never grow together. Neither do the new layers of wood grown from the stock and scion respectively unite. Instead of this, under normal conditions, they are produced in perfectly continuous layers. In the case of imperfect unions, however, the continuity of the new growth is more or less interrupted by the deposition of a certain amount of scar-tissue, such as serves in the healing of wounds. These conditions make the union mechanically weak; although the degree of mechanical strength varies from those (a large number) which are stronger than the adjacent parts of the same stem down to such as are incapable of even holding themselves in place.

In two recent papers (61: 1926; 62: 1928) PROEBSTING picked up WAUGH's work and, in addition to confirming the results noted above, found in some incompatible grafts, instead of the parenchyma layer usually present, <u>bark tissue</u>, extending nearly to the cambium contacts, resulting in mechanical weak-

ness and certain disturbances to the conducting systems. Great variation, however, was observed at the line of union. In grafts of stone fruits, HEPPNER and McCALLUM (36: 1927) and McCLINTOCK (54: 1925) also report some breakage at the line of union.

It appears, then, that the burden of the evidence points to the fact that in certain incompatible grafts, mechanical weakness at the point of union is a valid cause for failure. However, it would seem that this is neither the universal cause nor the most significant one, as shall be seen in the succeeding pages.

3. Nutritional disturbances

That the graft may result in profound nutritional disturbances of both stock and scion is indicated by a considerable mass of data, which will be considered under the headings of translocation, assimilation, differences in the complex organic constituents of the plant body, and protoplasmic toxemia. It must be borne in mind that these are by no means mutually exclusive groupings, but that there is necessarily a considerable amount of overlapping, inasmuch as the metabolism of the plant implies a unity and interrelation of its functions.

A. Interference with translocation

As regards the problem of translocation, there seems to be general agreement that the union, in certain cases, may result in interference to the upward flow of the crude sap, due principally to the faulty connection of the xylem vessels at the line of union. As has already been shown, PROEBSTING

(61: 1926; 62: 1928) found much scar-tissue and even bark-tissue extending across the line of union. Aside from the fact that this may mechanically interrupt the xylem elements, PROEBSTING finds that it may inhibit the cambium, with the consequent checking of the formation of new xylem, and that if not occluded, the vascular elements may be considerably distorted. This may or may not result in interference with the translocation of crude sap.

As early as 1788 DUHAMEL DU MONCEAU (22), however, had noticed that in unsuccessful grafts "the union had been made only by certain fibres, which have been able to support the scion in a state of verdure, and even to bear fruit, but the great number of the fibres were black and dry, and often I found at the line of union a gummy deposit, apparently resulting from the emanations of vessels which had never formed a union with those of the scion." He also noted a great folding and refolding of the vessels at the line of union. BOOTH in 1913 (9) attributes graft failures in part to the same cause, basing his conclusions also on the anatomy of the union. The data seem reasonably clear and sufficient to show that in general the graft union may mechanically so interrupt the upward translocation of water and mineral elements as to result in an insufficient supplying of these requisites to the scion.

With respect to the downward flow of the elaborated sap, there is even stronger evidence in favor of interruption at the line of union. The conclusions of DUHAMEL DU MONCEAU, BOOTH, and PROEBSTING, as stated in the preceding paragraph, apply equally to the transportation of crude and elaborated sap. Moreover, every investigator mentions the fact that in many

incompatible grafts there results a swelling, as of accumulated foods, immediately above the line of union, very similar to the effect produced on a tree by ringing or impeding the sap descent by a ligature. WEBBER's discussion (92: 1926) of this feature is carried to the point that he considers this swelling or its reciprocal as a criterion of the compátibility of the graft. Its effect on the mechanical strength of the union has already been noted. Suffice it to say that in few grafts, compatible or not, do we find the stem or the trunk of the same diameter at, above, and below the line of union. The fact of some interruption in the phloem in many incompatible grafts appearing reasonably certain, the problem remains whether this interruption be mechanical or physiological.

DANIEL (14: 1891; 16: 1899) advances a rather interesting hypothesis in regard to the translocation of certain nutritive elements across the line of union. He suggests that the contact of alien protoplasms results in the formation of different osmotic membranes which permit the passage of certain substances but restrict that of others. There is, as shall be seen later, some evidence to support such an hypothesis.

As in the case of the last proposition, one effect of the union of uncongenial bionts appears to be a restriction in the translocation of elaborated food materials. Whether this is merely mechanical or whether due to the selective action of osmotic membranes, the effect is the same--malnutrition of the stock.

B. Difficulty in assimilation

That the amount of the elaborated food furnished by the

scion may be either excessive or deficient for the proper nourishment of the stock is a point discussed by few investigators. BOOTH (9: 1913), however, considers it a valid cause for incompatibility. But failure of elaborated food to pass the line of union would functionally be the same as though the food were passing the line but in insufficient quantity. That this may occur has just been pointed out, and the effect on the stock noted. It is difficult to see how excessive food production could injure the stock. Moreover, as the stock is theoretically injured, its vigor, and consequently its absorbing power, are diminished, which in turn would act as a check on the amount of food elaborated. The stock would act as a safety-valve, and indirectly control the amount of food received. Hence it would seem that the above hypothesis is only partially sound. Deficient food for the stock, either actually or functionally, would have as its immediate result the weakening of the ensemble. From another aspect, however, this is the problem of the relative vigor of stock and scion to be discussed shortly.

The alternate possibility of excessive or insufficient crude sap furnished by the stock to the scion has aroused somewhat greater interest. The problem has already received some consideration under the discussion of translocation. Again BOOTH (9: 1913) considers this a valid cause for incompatibility. It is apparent that either excessive of deficient crude-sap supply might be deleterious. A number of investigators have noted the rather interesting fact that decreased water supply results in dwarfing of the scion, correlated with early flowering and fruiting and relatively short life. Advantage is

taken of this phenomenon in the growing of dwarf citrus trees. On the other hand, in certain cases the opposite effect may result from excessive water supply, the scion vegetating luxuriously but setting little fruit.

That the leaves of the scion may experience difficulty in elaborating the sap taken up by the roots of the stock is a problem of some controversy. BROWN (11: 1916) considers this a deciding factor in whether the graft will "take" or be unsuccessful from the start. If this is so, it is also likely that this may be a limiting factor in such grafts as are only moderately successful. But it is doubtful if the xylem fluids of two closely related plants differ sufficiently in composition to warrant the conviction that this difference is a fundamental cause for incompatibility. There is no selective action by the roots, this being a function of the leaves, since the scion controls by physico-chemical laws the selection of water and mineral materials, and selects only what is suitable for its use.

The converse proposition to the last, that the roots of the stock may find difficulty in assimilating the plant food manufactured in the leaves of the scion, had received practically no consideration. Certainly this problem is open to inquiry, and probably constitutes a valid cause for incompatibility. It would seem that for the roots to assimilate the complex food-products elaborated in the leaves is a somewhat more questionable matter than for the leaves to utilize the crude, unmodified sap supplied by the roots. The question is certainly worthy of investigation.

Even though the stock and scion be approximately alike in

vigor, the availability of their mutual products at the time of need may well become a limiting factor in the success of the graft. DUPLESSIX (23: 1911) finds that: "if one insert a scion of Doux Normandie (blossoming in June) on a stock of Launette (blossoming in late April), the sap will ascend in the trunk six weeks before the scion is able to receive it. The tree may die. If it lives the sap will accumulate in the swelling at the base of the graft, and this swelling in its turn can become a cause of the death of the tree. --------- If the reverse be tried, the scion of the Launette will require sap when the Deux Normandie trunk is not able to provide it, and the scion of the Launette will perish, or it will grow slowly for want of feeding at a useful time." LINDEMUTH (49: 1901) comes to the same conclusions and agrees with DUPLESSIX that of the two possible combinations, the least undesirable is the early-starting scion on the late-starting stock. LINDEMUTH suggests that the bleeding resulting from the early run of sap with a dormant scion may well be an indirect cause of canker injuries; and it would seem that the point is well taken.

C. Differences in the complex organic constituents of the plant body

Finally, in considering the nutritional causes of incompatibility, a number of investigators have stated in different terms a more or less uniform problem of accommodation in the plant, which amounts essentially to an ill-defined difference in the chemical constituents of certain plant substances, such as the protoplasms, saps, by-products, elaborated foods, etc. As may be readily seen, this is to some extent a reconsidera-

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C. Differences in the [illegible] [illegible] constituents of the [illegible]

Finally, in considering the [illegible] process of [illegible], a number of [illegible] [illegible] [illegible] differences [illegible] [illegible] [illegible] [illegible] [illegible] plants, which [illegible] [illegible] [illegible] [illegible] in the chemical constituents of certain plant [illegible], [illegible] [illegible] [illegible], [illegible] [illegible] [illegible], [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] [illegible]

tion, in a different light, of some of the causes of disturbance noted previously. It is significant that in certain cases these theories are not supported by experimental evidence. Probably this is due to the complex and poorly understood nature of such chemical processes.

With extraordinary foresight and penetration, DUHAMEL DU MONCEAU in 1788 (22) stated that in "les tentatives infructeuses que j'ai faites, m'ont fait naître des réflexions sur un certain rapport d'organization ou une similitude de parties qui doit être nécessairement entre la greffe (scion) et le sujet (stock), sans lequel, ou elles ne reprennent absolutement point, ou, si elles reprennent, elles ne subsistent pas longtemps." DUHAMEL goes on to say that it is very natural to think that the different success of grafts depends on the different relative organization of the woods. Besides the anatomical differences in woods, there must be chemical differences in the solid parts. Thus the suc (juice, essence, etc.) is now red, now white, sometimes transparent, other times refined and gummy. "Our knowledge is too limited concerning the organization of plants to be able precisely to establish the results of a given stock on a given scion, but in general we can perceive that these differences, which extend almost to infinity, must, since they are more or less considerable, influence the success of the graft."

Considering the matter of nutrition from a somewhat different viewpoint, DANIEL (15: 1894) suggests that the problem of incompatibility is a matter of difference in functional capacities of stock and scion (different structure, special diastases, different composition of crude and elaborated saps, rates of ab-

[illegible]

[illegible]

sorption, transpiration, respiration, etc.) The desideratum in the graft is that the ratio of:

$$\frac{\text{Functional capacity of the absorbing apparatus of the plant furnishing the scion}}{\text{Functional capacity of the absorbing apparatus of the plant furnishing the stock}}$$

remain such that neither of the plants can pass the limits of dessication or of aqueous repletion, but always find in their environment the essential elements of their own substance in assimilable form. Any deviation from this desideratum amounts to incompatibility in the exact degree of deviation. DANIEL's interpretation of his evidence, which is considerable and carefully obtained, seems to be sound. It is a rather ponderous theory to manipulate, but DANIEL seems to have struck the undercurrent of the whole matter, and to have worked out the same principle suggested by DUHAMEL (22: 1788), BROWN (11: 1916), and WEBBER (92: 1926), in more or less detail. That this is the basis of nutritional incompatibility is reasonably evident. That the two plants, each with its specifically different protoplasm, nutritional regime, and metabolism rate, should express different and conflicting needs, seems entirely sound. And that the thwarting of these needs,due to the profound changes in the physico-chemical environment effected by the graft, should result in more or less radical modifications in the degree of success of the artificial symbiosis thus induced, is the inevitably logical conclusion.

4. Protoplasmic toxemia

Apparently this, to DANIEL, is not the only reason under-

lying incompatibility, and he projects a further explanation of graft failure, which will be discussed under the above caption. For a graft to succeed, according to DANIEL, the protoplasms of the stock and scion must, and need only have, their physical and chemical properties modified no further than a determined limit which leads to the poisoning, or annihilates the essential properties, of living substance. To be sure, this may be only another aspect of functional incapacity, but to the writer this feature presents striking analogies to the problem of anaphylaxis in animals, and in the light of KOSTOFF's work (46: 1928), resulting in the demonstration of antibodies in the graft union, it seems wholly probable and essential. Due to the juxtaposition of two more or less foreign protoplasms in the graft union, immediate and positive defense reactions would be the logical result; and this would, in not later reduced or modified, cause the ultimate death of the two bionts. It is known that the pollen of one plant may act as poison on another; and when this is true, if the two plants are grafted, they blight and die as if poisoned. Recalling BURBANK's analogy of sexual hybrids and grafts (12: 1909), it would seem as though the same elements are here at work, while in this light the importance of taxonomic relationship in grafting receives a ready explanation.

EFFECTS OF THE STOCK ON THE SCION AND OF THE SCION ON THE STOCK

1. Quantitative effects

Most of the remaining pages will be devoted to a consideration of the effects of the scion on the stock and of the

stock on the scion. Most authors have attempted to separate these into the subdivisions of quantitative and qualitative effects; but while this will be done to a certain extent, it should be borne in mind, first, that there must necessarily be considerable overlapping, since modification of the vigor of either symbiont will result in a number of apparently unconnected effects, and second, that what appears to be a qualitative effect may, on further analysis, prove to be only a quantitative one. Thus, if the fruit be improved in color, taste, or sugar content, this may either be due to a qualitative modification of the chemical processes of the scion, or it may be due merely to the increased production of sugar and acid, the result of the quantitative stimulation of the stock, i.e. be an effect such as might be produced by any improvement of environment.

A. Effect on vigor of symbionts

It is universally agreed that the vigor of the scion may be modified by its association with the stock. The consensus of opinion seems to be that grafting a weak scion onto a moderately vigorous stock tends to invigorate the scion, augmenting its rate and amount of growth and general health. As an example of this may be taken the case of almond on peach, in which the resulting symbiosis attains a size and vigor doubling that of either symbiont growing ungrafted. In fact KNIGHT (43: 1809) goes so far as to say that "the office of the stock is, in every sense of the word subservient, and it acts only in obedience to the impulse it receives from the branches. The only qualities,

therefore, which are wanting to form a perfect stock are vigor and hardiness." Many investigators have observed the same thing and also the opposite effect of grafting a strong, vigorous scion onto a weak stock.

But that vigor may, if excessive, cause the death of the scion, was first brought out by DUHAMEL (22: 1788). Of plum and almond, the plum is the more vigorous. Hence the death of plum on almond is readily explained on the basis of an insufficient quantity of crude sap. This is further demonstrated by the fact that if the scion of this particular graft be kept severely pruned, its life is extended indefinitely, the needs of the abbreviated top being kept down to the capacity of the stock to supply. The reciprocal graft, almond on plum, however, is equally unsuccessful, but for the opposite reason. An excessive amount of crude sap is supplied, so excessive in fact that it can often be seen to ooze out at the line of union, and be deposited as a gummy mass. Aside from the fact that this layer offers an excellent culture medium and mode of ingress for vegetable pathogens, the significance of this oversupply of sap cannot be underrated. As a conclusive check on this deduction, DUHAMEL grafted the vigorous plums onto very large almonds. Ordinarily the almond would be unable to supply the plum with enough crude sap. Here, however, the reverse was true; and as might be expected, the scions soon dies, the decease being significantly accompanied by gummy deposits at the line of union.

VARD (87: 1891) and BURBANK (12: 1909) claim that this is a reciprocal effect, and that freqeuntly the scion may influence the tree on which it is growing, increasing its foliage, streng-

thening its roots, and otherwise making it more thrifty, the stock participating in large measure in the robustness or delicacy of the scion which has been imposed upon it. A suggested example of this last is the increased growth of Bartlett pear when topworked with Japanese pear. There can be no doubt but that the artificial symbiosis effected by the graft may result in much modification of the vigor of at least the scion, and probably also of the stock.

B. Effect on size of scion

Closely related to this point is the effect on the size of the scion. That this may at times be affected is unanimously agreed. In fact this is the principle underlying the production of dwarfed fruit trees, so widely practiced, especially in Japan. Thus there are many types of apple that, when used as stocks, inhibit the growth of the scion (SHAW, 84: 1919), for example Paradise and Doucin stocks (RIKER, 70: 1928). In citrus fruits, Navel oranges are frequently dwarfed on sour orange roots, but do well on sweet roots (NEWMAN, 57: 1926). The pear is dwarfed by grafting onto the quince, although in this case the flavor and size of the fruit are improved. The opposite effects may be observed. Thus "the common lilac (GARDNER, BRADFORD, and HOOKER, 24: 1922) is said to be greatly increased in stature on the ash, although this is a short lived graft."

This raises the interesting problem as to what characteristic of the union causes this excessive or reduced growth. It is known that the same stock may invigorate and increase the size of some scions and dwarf others. According to BAILEY (3: 1915)

and BREGGER (10: 1924), the size of the stock is the determining factor; and the above mentioned lilac on ash seems to bear this out, while others, as DANIEL (19: 1914), suggest that the congeniality of stock and scion is the factor at work. Doubtless both factors are concerned, but it is a matter of common observation that if a rapidly-growing scion is grafted onto a slow-growing stock, the resulting tree will be dwarfed; and if the reverse is true, the tree may be increased in stature, although in either case the graft is a short-lived one.

C. Effect on size of fruit

In some cases it seems evident that the size of the fruit may be affected by the nature of the graft. GARDNER, BRADFORD, and HOOKER (24: 1922) noncommittally mention numerous reports of this. KNIGHT (44: 1841), WEBBER (91: 1922), and ROGERS (74: 1927) observe that the more vigorous stocks have a tendency to produce larger fruits (pome and citrus), while BAILEY (4: 1898) notes the same effect from the use of less vigorous stocks (pear on quince). SHAW (84: 1919) also attributes changes in fruit size to the use of dwarfing stocks. Thus it would hardly seem that the size of the fruit is definitely correlated with the vigor of the stock; and furthermore it must be borne in mind that many factors affect this characteristic of the fruit, acting simultaneously and often at cross-purposes.

D. Effect on amount of yield

Of the same general nature is the detail of the amount of yield. Many workers have found that grafting may increase this, while HATTON (32: 1927), working with pome fruits, observed

that on one rootstock the same variety may fruit ten times as heavily as on another. This is not usually attributed to any one factor of the graft; but there is a certain correlation observable between dwarfed trees, increased yield, and short life. Apparently the same factors as influence the general vigor of the tree are here at work, although perfect congeniality may not necessarily increase the yield, since this frequently results in excessive vegetation at the expense of fruit formation. An example of this (SAHUT, 79: 1885) is the case of Chionanthus virginica on ash, which flowers abundantly but never fruits, while when grown ungrafted it bears. For this reason a moderately incompatible graft is often superior to a wholly compatible one.

It is rather interesting to note here the same conclusions coming from the rubber industry. In the Dutch East Indies the problem of grafting rubber trees is of vital importance, and a source of much controversy. Two papers (HENRY, 35, and HEUSSER, 38) in 1926 have dealt with the problem; and in both we find the same statement that grafting or budding rubber trees from selected clonal stock increases the yield of latex.

E. Change of habit of scion

The most peculiar effect of stock on scion is the changing of the form or habit of the latter. BAILEY (4: 1898), JOST (42: 1907), and KNIGHT (44: 1841) have observed this effect in various grafts, while GARDNER, BRADFORD, and HOOKER (24: 1922) report that a rambling habit may be changed to an upright one and the shape of the tree considerably modified.

[illegible] heavily [illegible] one year. This is not readily accounted for on any one factor of the grafts, but there is a possibility that [illegible] several [illegible] were grafted [illegible] later. [illegible] the stock [illegible] influence the [illegible] vigour of the tree [illegible] although it does not [illegible] [illegible] on the yield. [illegible] results, in [illegible] weight [illegible] in the case of [illegible] [illegible] in the case of [illegible] which [illegible] fruits, while [illegible] grown [illegible] a [illegible] is often [illegible] as a [illegible].

In the present [illegible] however, [illegible] from the [illegible] industry. [illegible] the [illegible] of [illegible] and a [illegible] of [illegible] (Hatton, 30, and [illegible]) have dealt with the problem, and it [illegible] the same statement that [illegible] stocks [illegible] increased the yield of [illegible].

1. Change of habit of scion.

The most peculiar effect of stock on scion is the [illegible] of the form or habit of the [illegible]. [illegible] (17. 1900), [illegible] (18. 1907), and [illegible] (19. 1921), have observed this effect in various species, while [illegible], and [illegible] report that [illegible] and the shape of the tree considerably modified.

F. Effect on the hardiness of the symbionts

That the hardiness of the plant is affected by grafting is pointed out by CARD (13: 1906), SHAW (84: 1919), and a number of other investigators. VARD (87: 1891), as has been noted, considers that the scion frequently modifies the stock, and when he finds that tender roses on hardy roses are killed, accounts for it by attributing it to the stock's loss of hardiness as a result of scion influence. It is well known to fruit growers that hardiness in the stock may be increased by grafting onto hardy stocks (usually stocks which induce early maturity), grafting being frequently employed for the purpose of saving delicate trees from winter-killing.

G. Effect on root system

The effect of the scion on the root system of the stock has been variously interpreted. BAILEY (3: 1915) reports that in certain grafts the scion may cause the roots to strike deeper and attain a greater degree of development. On the other hand, GARDNER, BRADFORD, and HOOKER (24: 1922) find that the root system may be inhibited by a vigorous top. The condition of the roots is obviously an important factor in the success of the association, and a series of careful investigations of the root-systems of grafted and ungrafted plants of the same age would be a valuable aid in drawing conclusions on this topic.

H. Modifications of the time schedule of the scion

Numerous modifications of the time schedule of the plant may be effected by the graft relationship, both with regard to the yearly and life developmental cycles. A few of these will be briefly considered in the next few pages.

5. Effect on the hardiness of the [illegible]

That the [illegible] is [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] [illegible]

[illegible]

[illegible]

[illegible]

c. Modifications of the [illegible] of the [illegible]

Climatic conditions [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] [illegible]

In the first place, the season of year of certain functions of the tree, such as leafing, blossoming, and fruiting, may be either retarded or advanced as a result of grafting. There is much agreement that such changes do occur. The relation between the type of stock and the time of these functions is a matter of some disagreement. With grapes the time of year of ripening is materially affected by the congeniality of the stock and scion (HUSMANN, 41). With peaches and almonds on certain plums the fruiting season is retarded, according to BROWN (11: 1916), while with the reciprocal grafts the season is advanced. SHAW (84: 1919) also finds that the season of fruit maturity may be affected by certain stocks. The interesting problem arises whether this earliness or lateness of the scion, due to the root-stock, bears any consistent relation to the season of the root-stock itself when grown unworked. BAILEY (4: 1898) believes that it does, and HOWARD (39: 1924) states that the ripening season of the same variety of plum on early, medium, and late peach is advanced or retarded accordingly, although HATTON and GRUB (33: 1926), in some careful work on many apple and plum grafts, could find no such relation evident.

A still more important and significant problem is whether the time in years from seed to bearing is affected by the stock. Looked at in another light, if there is no such effect, the propagator must select scions from bearing trees or else wait till the parent tree bears before expecting fruit from the grafted one. If the seedling apple tree bears at the age of eight years, will scions from three year old trees require an interval of five years before they set fruit? If this is so,

it would seem that the scion retains the "protoplasmic age" of the parent tree; and hence if an apple tree lives for two hundred years, scions from a one hundred and fifty year old tree would develop normally into trees which would fruit at once, but would become senile at the age of approximately fifty years. Since many of our most desirable varieties of fruit have originated from single trees, and have been propagated entirely by vegetative means, this would mean that such varieties will entirely die out within the normal lifetime of the parent tree. This resolves itself, then, into the problem of whether the protoplasm of the scion plant is all of one age or state of maturity; and if so, whether the protoplasm of the scion can be rejuvenated by its association with the stock. KNIGHT (44: 1841) held to the above mentioned view, although curiously enough he did not consider that it applied to root-cuttings. PUVIS in 1837 (64) opposed KNIGHT's view with considerable data, finding that "the variety grafted onto young trees successively, renews at each graft its vigor, and receives, to some extent a new life. This lasts much longer than that of the type." Other experimenters have also, by careful work, pointed out this same error in KNIGHT's deductions. Thus VOECHTING (in 52) grafted a bud of a two year old beet onto a one year old stock. The scion would normally develop into a flowering stalk the second year, but, due to the influence of the immature stock, it instead developed into a normal first-year leafy shoot with no flowers. TIMPE (in 52) demonstrated that seedling scions on old trees fruit at once, while seedling scions on seedling stocks or fruiting scions on seedling stocks fruit only after several years. BAILEY

(4: 1898) reports that scions from young trees set sooner if grafted onto old stocks. These data all indicate definitely that the scion partakes of the age of the stock.

It must be allowed that any influence of the stock in causing the early death of the tree through lack of nourishment could hardly be considered as modifying the chemical nature of the protoplasm of the scion in such a way as to induce premature but typical senility. With this fact in mind, the evidence of a number of authorities on the effects of "dwarfing stocks" is in agreement in the fact that dwarfing stocks hasten the period of fruiting, but at the same time shorten the life cycle of the scion. On the other hand, it has been pointed out that in certain cases the longevity of the scion may be increased by favorable grafting. But there seems to be general agreement that the duration of life of the graft is a fair index to congeniality.

A rather interesting problem arises in the light of the foregoing conclusions. Granted that the stock may influence the life duration of the scion, is it possible that a perennial stock may induce the perennial habit in an annual or biennial scion? That the converse is not demonstrable by experiment is obvious, since death of the stock must necessarily result in death of the complex. Considering the possibilities of:

(a) $\dfrac{\text{Annual}}{\text{Biennial or perennial}}$ (b) $\dfrac{\text{Biennial}}{\text{Biennial or perennial}}$

(c) $\dfrac{\text{Biennial or perennial}}{\text{Annual}}$

"c" immediately falls into the class just mentioned. DANIEL

(15: 1894) found that "a" was annual with partial or total death of the stock at the end of the first year, while the same was essentially true of "b" at the end of the second year. But in 1901 LINDEMUTH (49) had already shown that Modiola caroliniana (annual) on Abutilon thompsoni (perennial) lived for three years and five months, while Althaea narbonensis, a perennial, but one which survives only by the roots, on Abutilon thompsoni (perennial) had lived for over a year and was in excellent health at the time of writing. It is hardly necessary to point out the significance of these data, which demonstrate that in certain cases at least the effect of the stock is most profound in influencing the habits of the scion.

I. Modification of resistance to disease

The matter of resistance to disease in the graft association is a rather complex and indefinite one, when one considers the various types of disease, some of parasitic, others of autogenic origin, some affecting roots, others stems and leaves, some being caused by a definite, known parasite, others by an intangible virus. But this is an extremely important problem to the horticulturist. The significance of the problem will be seen when one recalls some of the more striking diseases of plants which are commonly grafted, as for example the attacks of Phylloxera on the grape, especially of southern Europe, the Wooly Apple Aphis, particularly in Australia, and the possibilities of transmitting mosaic diseases through grafting.

Experience has shown that it is possible to control various diseases by the use of disease-resistant stocks, since different

grafts vary in their resistance to the same disease. HENRY (35: 1926), working on the problem in the rubber tree, places grafting on a par with controlled pollination for combining in the plant disease-resistance and high latex yield. Viewed from the standpoint of congeniality, the problem presents further difficulties, for the innate resistance of the stock and scion may be influenced by the degree of success of the symbiosis, i.e. by the compatibility of the graft. It is very certain that general ill-health, such as would be the result of uncongenial grafting, would increase the susceptitility of the plant to the invasions of pathogens, as has been pointed out by HUSMANN (41) in grapes, and WEBBER (92: 1926) in citrus fruits.

J. Direct transmission of disease

But the question of transmission of disease directly from stock to scion or from scion to stock, through the graft, is not the simple matter it might seem at first glance. If chlorosis or variegation be due to a virus, inhibiting chlorophyll-formation, it ranks with other causes in the pathogenic class. BAUR (in 52) finds that the chlorosis in Abutilon thompsoni, which he demonstrates is due to such a virus, is transmissible from stock to scion. Certain strains of Abutilon are resistant to the virus, and BAUR observes that if a chlorotic stock is topped with an immune strain, and if this latter is again top-worked with a green but susceptible shoot, the virus is transmitted through the immune shoot and becomes evident in the susceptible one. Working with the disease "Pecan Rosette", ORTON (59: 1914) finds that healthy scions on rosetted stocks

invariably developed the disease unless the stock meanwhile recovered, while rosetted scions on healthy stocks attained normal development except for the customary rosetting of all nursery stock. Working with the mosaic disease of Irish potato, SCHULTZ (82: 1919) shows that healthy potatoes on mosaic stocks are infected by the stocks; while in the reciprocal graft, the disease is also transmitted from scion to stock. In fact, grafting is often a successful method of inoculation with mosaic where the customary methods fail. This evidence all seems to point to the fact that diseases due to a virus are generally transmitted from the diseased biont to the healthy one, the transmission from stock to scion being the more marked.

2. Qualitative effects

A. Transfer of complex organic constituents across the line of union

The next few pages will be devoted to a consideration of certain qualitative reciprocal effects, remembering, as has been noted, the comparative insufficiency of our term "qualitative". In the first place, a qualitative influence would be inconceivable without the transportation of certain complex chemical substances from one to the other of the bionts. This matter has been the subject of a great deal of investigation in the last few years; and much evidence is advanced to show that some substances are translocated, while others are not. Chief among the evidence are the data following:

Chemical substance investigated:	Plants grafted:	Transportation:	Investigator:	Year:	Reference:
Atropin	Datura on potato	+	Strasburger	1885	28
Inulin	Compositae	-	Daniel	1891	14
Starch & sugar	Turnip on cabbage	-	"	1894	15
Starch	Potato on Datura	-	Lindemuth	1901	19
	" " Capsicum	-			
	" " S.pseudo-capsicum	-			
Atropin	Belladonna on tomato	+	Laurent	1905	28
"	Tomato on belladonna	-	"	1906	28
Nicotin	N. affinis on N. tabacum	+	Grafe u. Lensbauer	1906	28
	N. tabacum on N. affinis	+			
Anthocyanin	Legumes	-	Guignard	1907	28
Alkaloids	Atropa & Datura on Solanum & Lycopersicum	+	"	1907	28
Anthocyanin	Rosaceae	+	"	1907	28
	Cotoneaster & Photinia on wild quince	-	"	1907	28
Albumen	Epiphyllum on Pereskia	+	Mitosch		52
Atropin	Datura on potato	-	Meyer & Smith		52
Factor controlling variegation	Ulmus, Acer, Weigelia	-	Timpe		52
Chlorosis-inducing-virus	Abutilon	+	Baur		52
Capsicin	Tomato on eggplant	-	Daniel	1914	19
Anthocyanin	Phaseolus lunatus on P. vulgaris	-	Richmond	1926	69
"	"	-	Hoffmann	1927	38

The work of RICHMOND (69: 1926) and HOFFMANN (38: 1927) throws a most interesting light on the question of transfer across the graft union. Beside their results noted above, these investigators also found the bacterial specificity of the legumes indicated markedly altered. Thus _P. lunatus_ is specific for one nodule bacterium, _P. vulgaris_ for another. The seeds of the grafted plant are not specific for either; and their seedlings will have nodules formed by either or both strains of bacteria. This would seem to imply the transfer of some substance such as would modify the protoplasm to such an extent as would destroy the incompatibility existing between the ungrafted scion plant and the alien nodule organism.

From this mass of data it is possible to draw several conclusions. In the first place, the chemical autonomy of stock and scion is such that each, individually, produces certain chemical end-products not normally found in the other. In addition to these products, there are substances present which are more or less common to both, which substances are essential to life. At the line of union, in successful grafts, this second group of more essential substances is passed readily from scion to stock; while in spite of the transportation of substances necessary for nutrition and development of the individuals associated by the graft, certain other apparently less essential and perhaps even harmful substances can in some cases remain localized in one or the other of the conjoints.

B. Qualitative alteration of the fruit and other plant organs

In considering the question of the qualitative alteration

of the fruit, which is of course of extreme importance to the grower, there is great difficulty in determining whether differences in color, taste, amount of sugar and acid, etc., are actually qualitative, or merely due to an improved environment. Moreover the criteria for determining quality are not always strictly scientific. Thus taste is a vague sense, about which few people will agree; and tasting is the method generally employed in judging fruit quality.

KNIGHT (43: 1809) felt that "no improvement ever was or will be produced by propagating from scions on stocks of different species. The goodness of the fruit is never affected by any stock of the same species." LORD BACON had previously asserted that "fruits can be improved by combining the excellencies of different kinds, but this cannot be done by grafting, because the graft (scion) wholly overruleth the stock." On the other hand, PLINY indicated the marked improvement of grafted chestnuts. OLIVIER DE SERRES asserted that by repeated grafting "les fruits s'en diversifient et bigarrent." LE GENDRE and later QUINTINIE showed that Bon Chretien pear must be grafted onto wild quince, because as a seedling it produces a speckled, small, and rough fruit. According to DANIEL (15: 1894), "there is no doubt that these variations in taste must correspond to changes in the chemistry of the plant, which when grafted loses fatally its autonomy and becomes dependent on its conjoint." SAHUT (79: 1885) feels that "generally the influence of the stock has for its happy result the rendering of the fruiting more abundant, augmenting its volume, and improving its quality." (trans.), while GARDNER, BRADFORD, and HOOKER (24: 1922), although consid-

ering it a strictly quantitative effect, allow that the quality and taste of a given fruit vary with the stock employed. BROWN (11: 1916) also finds the color and flavor influenced by the graft symbiont, and states evidence to demonstrate increased sugar content in Baldwin apples when grafted onto Tolman Sweet apples. Moreover, the keeping quality appears to be affected, as witness the case of Duchess apples on the Ben Davis variety, in which the fruit keeps much longer than if the Duchess is grown on its own roots or on certain other stocks.

As to actual tests of the chemical constituents of the grafted fruits, we have work by a number of investigators. HUSMANN (41) in 2000 acid and sugar determinations of two hundred and seventy-one varieties of grapes grafted onto various stocks, finds a close correlation between the saccharine and acid constituents of the fruit and the compatibility of the graft. Where high sugar and acid determinations were shown, the congeniality and adaptability were both good, and stock and scion seemed suited to the existing conditions. LAURENT (in 52) notes that grafted cabbage forms contain an increase in crude fibre and saccharine matter and decrease in total ash, although certain ash constituents were increased. Moreover grapes vary in their composition when grafted onto different stocks. RIVIERE and BAILKACHE (in 52) assert that variations in color, size, and content of sugar and acid, and also dry matter in apples and pears occur when worked on different stocks, and grapes show marked differences in the sugar and acid content of the juice.

Closely related to these findings are those of DANIEL and others with reference to stem, leaf, and flower characteristics.

In DANIEL's grafts of _Myosotis_ and _Mertensia_ on cabbage, and _Kleinia_ on _Cineraria_ (20: 1927), he found that the flowers, leaves, and stems became variously modified. He likewise found that the leaves of tomato on pimento are clearly different from those of tomato on egg-plant. The fruits of the latter are more agreeable than those of the tomato seedlings, and those of the tomato on pimento are still more so. _Prunus piscardii_ on _P. americana_ develops much more highly colored foliage than _P. piscardii_ on _P. domestica_, according to BAILEY (4; 1898). All of the above data on fruit, flower, stem, and leaf modification lead to the same conclusions, i.e. that the qualities of these organs may become considerably changed due to quantitative differences in the stock. And since frequently well-nourished and poorly-nourished seedlings do not show the differences in these organs that appear in grafts of the same scion on different stocks (McCALLUM, 52: 1909), it may be concluded that in some cases at least the stock so modifies the nature of the scion as to effect definitely qualitative changes in the characteristics of the latter.

C. Qualitative effects demonstrated by double-grafting

The practice of double-grafting, i.e. of grafting a shoot onto the scion of an existing graft, brings to light the effects of a number of influences, in general decidedly qualitative in nature. A few examples will be given. DUHAMEL DU MONCEAU (22: 1788) reported some success with grafting pear on thorn on pear; but one of his most ingenious experiments, performed to disprove the theory of graft-hybrids to be sure, is worthy

of note. He grafted _butter-pear_ onto _wild-pear_ and found that no change occurred in the scion. He then proceeded to topgraft this with a scion of _wild-pear_. The tree produced _wild-pears_. This was followed by grafting onto the last a shoot of _butter-pear_ again; and the procedure was repeated indefinitely without altering the nature of the respective fruits.

In 1885 SAHUT (81) found that both stock and intermediate are subject to the influence of the second scion. PFRIMMER (60: 1885), a French fruit-grower, reported that _Citrus nobilis_ on citron grows very rapidly the first year, fruits the second, and dies the third. _C. nobilis_ on wild quince grows miserably. But _C. nobilis_ in wild quince on citron had been successful for seven years at the time of writing. ABRIAL (1: 1914), another French worker, reported that Jules d'Airolles pear on Bergamotte Crassane on wild quince bore fruit from two to three times as heavy as and different in appearance from those of a nearby Jules d'Airolles pear grafted directly onto wild quince. GRUBB (27: 1927), in England, performed a number of double-grafts on pear; and he writes that the variety used as an intermediary has a distinct influence on the second scion. Moreover this influence of the intermediary, which is not always correlated with the vigor of the intermediary, probably affects the age at which the tree begins to bear fruit. R. C. KNIGHT (45: 1927), working from the same station, finds the intermediary playing a considerable part in influencing the scion; this part, however, he considers as quantitative. He goes farther to point out that the vegetative union of a scion with two stocks of different characteristics produces a tree, the vigor of which is intermed-

iate in type; but the factors coming from the stock or stocks which govern blossoming do not appear to be evenly blended.

That there is any influence of the intermediary on the scion is strong evidence of the qualitative effect of stock on scion. In general, from the above data, it would seem as though we have here a definite indication of such influence.

D. Qualitative effects demonstrated by reciprocal-grafting

Interesting light should be thrown on this problem by a consideration of the comparison of the behavior of grafts with that of their reciprocals. A number of references have already been made to such grafts, and the literature is replete with examples of the same. In general the opinion seems to be that the success or failure of a graft is in no way correlated with the success or failure of its reciprocal. The work on mosaics has shown that the transferral of the disease is very dependent on whether the diseased part is stock or scion. Similarly DANIEL (17: 1913) found in reciprocal grafts of Black Belgian bean, which rapidly becomes chlorotic in nutrient solution, and the Soissons bean, which retains its green color much longer, that where the Belgian bean was used as stock, the plant became chlorotic much sooner than controls, and when used as scion, much later.

In 1926 WEBBER (92) pointed out that while in lemons or sweet oranges on the trifoliate orange (<u>Poncirus trifoliata</u>) the stock grows much more rapidly than the scion, in the reciprocal graft the effect is much more pronounced. DANIEL (17: 1910) states that pear on wild quince succeeds while its reciprocal in-

variably fails; and his work also shows the inequality of reciprocal grafts of potato, Belladonna and tomato. Likewise most Japanese plums can be grafted onto most European plums, but the reciprocals generally fail.

Thus it is seen that reciprocal grafts do not invariably present the same degree of success, and that there seems to be at times pronounced uncongeniality in a graft whose opposite is congenial. It seems reasonably certain that this is not entirely a question of more or less vigor in stock and scion, although that appears to be the explanation in some cases, but that we may sometimes find the answer in the physico-chemical changes of the new symbiotic environment.

"GRAFT HYBRIDS"

1. Data

There have been a number of cases reported of so-called "graft hybrids". It is unfortunate that this term should have been applied, for in origin, in appearance, and in theoretical significance they differ radically from sexual hybrids. The term "graft hybrid" would imply a plant resulting from the fusion of two vegetative cells and of a homogeneous nature, more or less intermediate between the two parents. Such is not the case in the present instance, however. If such a plant is the result of specific influence of stock on scion, it would be a qualitative effect par excellence. But again there is great question whether the "graft hybrids" are the product of such specific influence.

A considerable number of "graft hybrids" occur, and a few

of them will be described, since an analysis of their significance is entirely an individual matter. Best known of all is _Crataego-Mespilus_, a product of the graft of _C. monogyna_ (hawthorn) and _M. germanica_ (medlar). It produces branches like those of each parent, and at the same time branches wholly intermediate in type. Two varieties have been segregated and named _C. Dardari_ and _C. Asnieresii_. The seeds of these plants throw back to one or the other of the parents, although cuttings remain true to type.

Laburnum (_Cytisus_) _Adami(i)_ arose from a graft of _L. vulgare_ and _C. purpureus_. It has two varieties, as has _Crataego-Mespilus_, and presents the same general characteristics. (REHDER, 65: 1915)

WINKLER (95-98) deliberately stimulated the production of _Solanaceous_ graft hybrids by permitting only the buds exactly at the line of union to develop. Two or three of these deserve mention. _S. nigro-lycopersicum_ (_S. nigrum_ on _S. lycopersicum_) resembles a nightshade and a tomato longitudinally united. _S. tubingense_, of the same parentage as the above, is of the type of _Crataego-Mespilus_. _S. Darwinianum_, also of the same origin, presents almost a perfect blending of characters, i.e. comes closest to the nature of a true hybrid.

Beside these, many other plants have produced similar offshoots. The Bizziaria orange and the Trifacial orange are of this type; while grapes, hyacinths, roses, and potatoes have yielded the same sort of progeny. (DARWIN, 21: 1890)

2. WINKLER's classification of hybrids

A number of explanations of these phenomena have been suggested, some of them based on sound scientific investigation.

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WINKLER, in 1910 (96), proposed the following theoretical classification of hybrids:

1. Sexual hybrids.
2. Graft hybrids, arising by:
    A. Fusion of somatic cells (Verschmelzungs Pfropfbastarde);
    B. Specific influence of one graft symbiont on the other without cell fusion (as by chemical substances, plasma-transfer, etc.)--Beeinflussings Pfropfbastarde);
    C. Combinations of cells without altered individuality (chimaeras) of the type:
        a. Sectorial chimaeras, in which the cells of the vegetative point are separated by longitudinal planes;
        b. Periclinal chimaeras, in which the periclinal layers of the vegetative point are developed, some from one, some from the other parent;
        c. Hyperchimaeras, in which the vegetative point is a mosaic of the cells of both parent races.

WINKLER, in another paper (98: 1910), had previously pointed out that the character of graft hybrids may be determined by their chromosome numbers. Suppose two plants X and Y respectively, with diploid (somatic) chromosome numbers x and y. The germ cells would have $\frac{x}{2}$ and $\frac{y}{2}$ as their numbers. If the offspring is a sexual hybrid, it will have as a diploid number $\frac{x+y}{2}$. This would become in the haploid stage $\frac{x+y}{4}$. Thus if we examine the cells (somatic) of a sexual hybrid, we expect to find for the

chromosome number that of one parent or a number intermediate between those of both parents. If instead we examine the cells of the graft hybrid, we could tell by comparison with those of the parents whether we have a true graft hybrid (of WINKLER's fusion type), a sexual hybrid, or a chimaera. A sexual hybrid would have $\frac{x+y}{2}$ chromosomes in all its somatic cells. The chimaera would have x chromosomes in some cells and y chromosomes in others. If in both parents the number was the same, the hybrid and chimaera could still be separated by morphological characters, since the hybrid would present a blending of characters, while the parent influences of the chimaera would stand out sharply against each other. On the other hand, the fusion graft hybrid would have x+y chromosomes in all somatic cells, since the fusion of two somatic cells would not be preceded by reduction.

3. WINKLER's classification applied to these data

On the basis of this method, accompanied by a careful examination of the morphology, the graft hybrids described are found to fall into one or another of WINKLER's three subdivisions. True fusion of two somatic cells appears to have occurred in *S. Darwinianum*. The chromosome number is double and the characters are blended. *S. nigro-lycopersicum*, as would be expected, is a sectorial chimaera, the cells forming one side of the plant, coming from parent, having united mechanically with a complementary half from the other parent. No fusion took place. All the other graft hybrids described fall into the class of periclinal chimaeras, having an *epidermis* one or two cells thick formed from one parent, while the remainder of the plant is purely the other parent.

The seeds of these periclinal chimaeras throw back to one or the other of the parents. This is readily explained (BAUR, 5: 1910) on the basis of the genesis of the germ cells. Since these cells always arise from the first subepidermal layer of cells, the character of the latter will determine the character of the offspring. Thus _Crataego-Mespilus_ seeds are all pure for _Crataegus_, since the plant is essentially a _Crataegus_ in a _Mespilus_ epidermis one cell thick, and the germ cells form from _Crataegus_ tissue. The reverse is true, however, of _C. Dardari_, which differs from _Crataego-Mespilus_ only in having a _Mespilus_ epidermis two cells thick. The germ cells in this case are formed from _Mespilus_ cells, and hence are true for _Mespilus_.

As to the origin of these plants there is some controversy. There are three possibilities of their origin (STRASBURGER, 85: 1901): Either full fusion of protoplasts of stock and scion took place, there was some specific influence of stock on scion or _vice versa_, or there was an adventitious bud formed at the line of union, composed of mixed cells of both bionts.

Returning to WINKLER's classification, the following explanation seems most satisfactory:

A. _Fusion of somatic cells_: "The cells of two essentially different species can unite in other ways than sexually, and serve as the primordium of an organism which develops independently, but in a most intimate association, the properties of the two parent strains" (WINKLER, 96: 1910). (_S. Darwinianum_)

B. _Specific influence_ does not seem necessary in order to explain the graft hybrids thus far reported.

The nature of these pathological changes, [illegible] is one of the [illegible] of the [illegible]. [illegible] (1930) [illegible]

[illegible]

[illegible] *differs from* [illegible] [illegible] [illegible]

[illegible]

[illegible] a [illegible] of [illegible] is [illegible]

[illegible] possibilities of [illegible] (1933). [illegible]

[illegible]

According to [illegible] classification, the following [illegible]

(a) *Pattern of specific cells.* The cells of the [illegible] [illegible]

[illegible]

(b) *Specific influence* [illegible]

C. <u>Combinations of cells without altered individuality</u>: The possible arrangement of such cells accidentally thrown together in the cell-complex resulting in the adventitious bud, or in normal juxtaposition in the cambium layer of common cells, would explain both types of chimaeras, according to the way in which such cells are placed in the vegetative tip. "Bud variation" is too vague a term to be used as an explanation of these cases; and furthermore such an explanation is unnecessary.

In concluding these remarks about graft hybrids, it would be well to recall the work of RICHMOND (69: 1926) and HOFFMANN (38: 1927) in altering the bacterial specificity of legumes (see page 32), which physiologically merits rank with the other graft hybrids mentioned.

DETERMINATION OF COMPATIBILITY

Until very recently it has been the general opinion that the only way of determining whether or not two given plants would graft successfully was by field trials. This has been asserted and reaffirmed by most of the leading authorities on the subject of grafting, usually as a matter of regret, for the trial and error method entails much loss of time and money. Very recently, however, there has been some work on the possibility of such determinations by means of sero-diagnosis or precipitin reactions. REVIS (68) suggested the use of such methods in 1923, for predicting the affinity of stock and scion in the grape. The method is essentially as follows: A quantity

of sap is expressed from the tree or vine at high pressure (of the order of 6000 lbs.). This may or may not be diluted. It is then injected into the peritoneum of rabbits at intervals and in varying dosages. The blood of the rabbit develops an immunity to the sap and with it the ability to precipitate its constituents. By determining differences in the precipitations of different saps, it was thought to establish a criterion for the degree of affinity of stock and scion.

GREEN in 1926 (26) tested with the precipitin reaction several families and genera known to be capable of intergrafting. Positive results were obtained with the genus Citrus, and within the subfamily Prunoideae and the family Solanaceae. Conversely, Beta vulgaris, Rheum officinale, and Olea Europa gave negative results with each of the immune sera of the other families investigated, correlated with the difficulty of intergrafting these with species from such families. The Pomoideae also gave negative results with the Prunoideae. The lack of success in intergrafting these two families is well known. However, his constant positive results in the Pomoideae and Prunoideae does not explain the difficulty in grafting apple and pear. Moreover, he could not differentiate between closely related species.

PROEBSTING and BARGER (63: 1927) confirm GREEN in their lack of ability to differentiate between closely related species by this method; and in attempting to distinguish Beauty plum, which makes a poor union with almond, from Santa Rosa plum, in which the opposite is true, they were unable to demonstrate any such difference in precipitin reaction. These experiments do not confirm GREEN's conclusions that the method can be used to

predict affinity; and it seems to the authors that the uniformity of the reaction in the reciprocal tests and in the comparative tests indicates that more refinements in procedure must be developed before these slight differences can be demonstrated.

EAST and KOSTOFF at Harvard are using a modification of the Abderhalden reaction of protein precipitation which has the advantage of eliminating the variability attendant on the use of two experimental organisms, i.e. the plant and the rabbit, and also serves to dispense with the variability in rabbits, which must be considerable. The method consists of precipitating certain elements of the expressed juice of one plant by the presence of the corresponding elements of the other.

SUMMARY OF DATA

On the basis of the graft-literature as indicated in the preceding pages, the following propositions seem to be justified:

1. In general, the degree of compatibility between stock and scion is definitely correlated with the degree of genetic relationship, the more successful unions as a rule being between plants of close phylogenetic affinity.
2. Of the causes of incompatibility suggested, the following are considered most fundamental:
   - A. In certain cases, mechanical weakness may lead to the failure of the plant to survive.
   - B. Nutritional disturbances are the basic cause for the ill results of most incompatible grafts. These may be due to:

a. Mechanical interference with translocation;

b. Failure of the scion to receive an adequate supply of crude materials at the time of greatest need;

c. Functional incapacity of one or both bionts to adapt themselves to the new physico-chemical environment effected by the artificial symbiosis.

C. In certain cases protoplasmic toxemia, analogous to anaphylaxis in animals, may be the cause of failure.

3. The effects of the association on the conjoints may be:

A. Quantitative in:

a. Modification of their size and vigor;

b. Modification of their adaptability to their environment;

c. Modification of their periodic cycles of development;

d. In come cases, inhibition of certain functions, as flowering and fruiting.

B. Qualitative in:

a. Interference with nutrition or exposure of the protoplasm to a foreign substance which may or may not be harmful;

b. Modification of the protoplasm or of its by-products, as is evidenced, for example, in double-grafting;

c. The frequent functional incapacity of the plant to act with equal success as scion and stock.

d. The production of certain radical modifications of the new growth, as is demonstrated in certain types of graft hybrids, if these be taken at face value.

4. At present there exists no satisfactory method for determining in advance the compatibility of two potential graft-conjoints. However, that sero-diagnosis or other physiological or chemical technique will ultimately offer such a method is well within the limits of probability.

THE GRAFT UNION: AN ANALYSIS OF THE RECIPROCAL EFFECT OF STOCK AND SCION

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